

A COMPARATIVE STUDY OF THE DOUBLE MOTOR INNERVATION IN MARINE CRUSTACEANS

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(With Ten Text-figures)

INTRODUCTION

IN previous publications (van Harreveld & Wiersma, 1936, 1937) it has been shown that the adductor muscle of the dactylopodite and the flexor of the propodite of the chelipeds of *Cambarus clarkii* and of *Astacus trowbridgii* are innervated by two motor axons only, each of which elicits a different kind of contraction. The experiments of Lucas (1907) suggest the existence of two kinds of motor fibres in other crustaceans, as he found two kinds of contractions in the adductor of *Homarus vulgaris*. The veratrin-like contractions which were obtained from different marine crustaceans by Wiersma (1933) when the nerve was stimulated with direct current of long duration also support this idea, though at that time a working hypothesis was proposed which assumed only one kind of motor fibre. Pantin (1934, 1936*a, b*) has applied this latter idea to different muscles of the walking legs of *Carcinus maenas* and to the "cutter" claw of this animal. For the adductor of the "crusher" claw he assumes the existence of a "double excitable" system.

In *Cambarus* the twitch contraction of the adductor increases steplike in height (van Harreveld & Wiersma, 1936). The first step of the twitch has a chronaxie of 0.3–0.5 σ , which is identical with that of the nerve fibre. The higher steps are due to repeated discharges in the twitch fibre. Wiersma (1933) found twitches which also increase steplike in the adductors of *Homarus vulgaris*, *Maja squinado* and *Cancer pagarus*; the same fact was observed by Wiersma & van Harreveld (1934) in *Eupagurus bernhardus*. The pseudo-chronaxie of the first visible contraction in these animals was much longer, in fact so long that at least a double discharge was assumed. In the following pages experiments are described which show that this assumption is correct for the adductors of the claw of *Randallia ornata* (brachyuran decapod) and *Blepharipoda occidentalis* (anomuran decapod), and that these muscles as well as the adductor of the walking leg¹ of *Cancer* *ithonyi* have a double motor innervation.

¹ Throughout this paper this expression is used as an abbreviation for the flexor of the dactylopodite, a muscle which is homologous with

the adductor of the cheliped.

THE DOUBLE MOTOR INNERVATION OF *RANDALLIA ORNATA*
(RANDALL) AND *BLEPHARIPODA OCCIDENTALIS* (RANDALL)

By staining the adductor muscles of *Randallia* and *Blepharipoda* with methylene blue we found a triplotomic branching (van Harreveld & Wiersma, 1937) in the first main division of the three axons near the muscle. We have shown for *Cambarus* that two of these fibres are motor axons giving, on stimulation, the slow and the fast contraction. The third fibre is an inhibiting axon. The triple innervation in the marine species makes it likely that the same situation exists here.

We used the method which was successful in the crayfish to isolate single, functioning axons. The nerve fibres were prepared in the meropodite while submerged in sea water. As in *Cambarus* this was done by splitting the nerve until single fibres were isolated (van Harreveld & Wiersma, 1936) and stimulating the axons thus obtained with micromanipulated electrodes. Both in *Randallia* and *Blepharipoda* there are only two fibres which on stimulation give a contraction of the adductor muscle. As in *Cambarus* a thick and a thin fibre can be distinguished; the ratio of the diameters was about 1.4 to 1 (see Table I), which is about the same as in the crayfish.

Table I. *Diameter of the motor fibres of the adductor muscles in the cheliped of Blepharipoda and Randallia and in the walking leg of Cancer*

	Fibre for fast contraction μ	Fibre for slow contraction μ	Ratio
<i>Blepharipoda</i>	39	28	1.4
	37	28	1.3
	31	23	1.3 ^b
	50	37	1.3 ^b
	35	25	1.4
	34	25	1.4
<i>Randallia</i>	39	28	1.4
<i>Cancer</i>	46	34	1.3 ^b
	51	34	1.5
	45	39	1.2
	28	18	1.5 ^b
	44	34	1.3

Stimulating each fibre separately with an induction coil, giving frequencies of 40–50 per sec., the difference between the two contractions obtained is not obvious. With other frequencies (obtained with a vacuum tube stimulator) the differences become more pronounced, the fast contraction shows the highest contraction with higher frequencies but with lower frequencies the slow contraction is the highest.

Muscle action currents have been recorded with a Matthews oscillograph on stimulation with different frequencies of the isolated fibres, especially in *Blepharipoda*. This stimulation always results in a row of action potentials; in the case of the thick fibre the first stimulus sets up a noticeable action potential, whereas such is not the case on stimulation of the fibre for the slow contraction (Fig. 1). In both cases the

action potentials grow in the course of the stimulation. In the fast contraction this growth is not very pronounced with the frequencies used (from 1 to 100 per sec.). The growth is greater when the frequency of the stimuli is higher. Below a frequency of 1 per sec. no growth of the action currents was observed. To obtain a mechanical contraction the frequency has to be more than about 20 per sec. Fig. 2 illustrates this.

On stimulation of the fibre for the slow contraction action currents become visible only after a number of stimuli; with high frequencies (100–150) they grow faster and become larger. In this animal, however, they never reached the size of the first action current of the fast contraction. With lower frequencies they are hard to distinguish from the current escape. For instance, in a preparation stimulated with frequency of 53 per sec. the 50th stimulus elicited a deflexion of about 0.7 mm., whereas the first stimulus of the fibre for the fast contraction caused a deflexion of

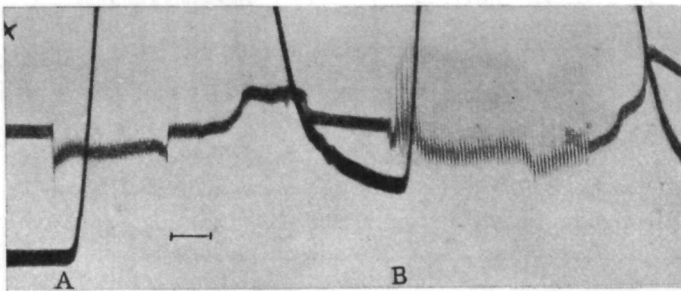


Fig. 1. Muscle action currents and isotonic mechanogram on stimulation of the thin (A) and the thick (B) motor fibre of the adductor muscle in *Blepharipoda* with a frequency of 53. The mechanical response on stimulation of the two fibres is almost the same. The action currents of the slow contraction are just visible at the end of the stimulation; the action currents of the fast contraction are large from the start. Time mark $\frac{1}{4}$ sec.

1.1 mm. The mechanical contraction in both cases was about the same, except for the somewhat longer latent period of the slow contraction.

SUMMATION OF TWO INDUCTION SHOCKS IN THE FIBRE FOR THE FAST CONTRACTION

Two pairs of electrodes were put either on the isolated thick fibre or into the meropodite, each connected with a separate induction coil, the primaries of which were broken at variable time intervals by a contact breaker. The direction of the current in both pairs of electrodes was descending. To avoid having an impulse pass a part of the nerve fibre that had recently been electrically stimulated, the first stimulus went to the proximal pair of electrodes, the second stimulus to the distal pair. In *Cambarus* no contraction ever resulted from the summation of two subliminal induction shocks (van Harreveld & Wiersma, 1936). In *Randallia* and *Blepharipoda* we succeeded in obtaining a contraction by summing two induction shocks, which, even in quite fresh and freely contracting preparations, did not give

any sign of contraction when given alone. As we found that two summated induction shocks applied to the whole nerve give exactly the same result as when applied to the isolated thick fibre, the fibre was usually not prepared. The thin fibre does not give

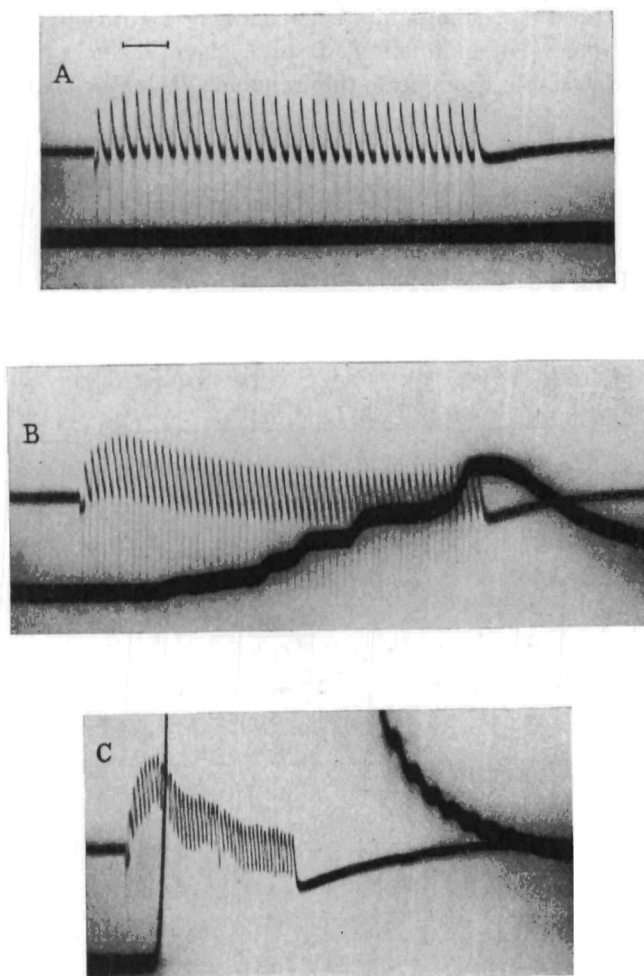


Fig. 2. Muscle action currents and isotonic mechanogram of the adductor of *Blepharipoda* on stimulating the fibre for the fast contraction with different frequencies. *A* frequency 17 per sec.; no mechanical response, some growth of the action currents. *B* frequency 30 per sec.; a small contraction results, a more pronounced growth of the spikes. *C* frequency 55 per sec.; a quick and high mechanical response, the action currents build up. Time mark $\frac{1}{2}$ sec.

a mechanical response on two summated induction shocks. The height of the contraction varies with the time interval between the two shocks. When the height of the summated contraction is plotted against the time interval it is found that a contraction occurs only within a relatively small range of intervals. Since conduction in the nerve fibre is fairly slow (about 5 m. per sec.), the conduction time between

the two pairs of electrodes becomes a substantial part of the minimum interval; thus the distance between the electrodes has a large influence on it. In *Randallia* the shortest "least interval" for which summation was observed was 2.3σ (electrode distance 7 mm.); the longest interval was about 10σ . In *Blepharipoda* the range of time intervals that can give summation is about the same. A curve relating height of contraction to interval of summing stimuli is given in Fig. 3 for *Randallia*. As we found that with faradic stimulation the frequency has to be about 20 per sec. to

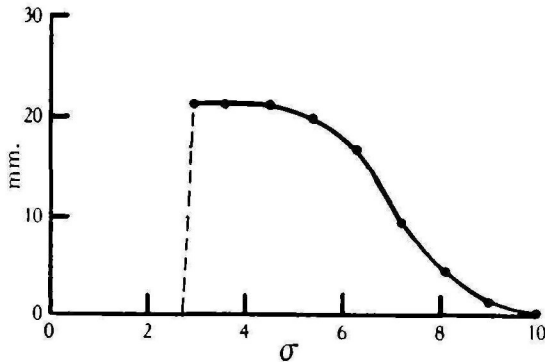


Fig. 3. Curve relating the height of the contraction and the time interval of two summing induction shocks in *Randallia*.

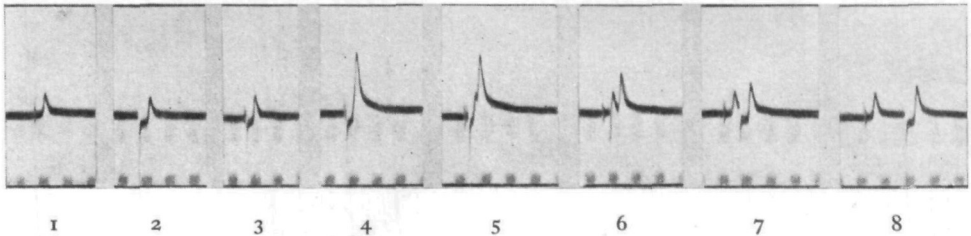


Fig. 4. Action currents in *Blepharipoda* on summation of two induction shocks. 1 and 2 are the action currents from single shocks given through the proximal and distal electrodes respectively. Coil distances 16 and 17 cm. Distance between the two pairs of electrodes 4 mm. In 3 the time interval of the summing shocks is 1.4σ ; no summation. In 4 the time interval is 1.6σ ; summation results, hardly any sign of the existence of two tops. In 5, 6, 7 and 8 the time intervals are respectively 3.6 , 7.2 , 14.4 and 34σ . Two tops occur, the second one decreases gradually in height, as the interval between the two induction shocks increases. Time $\frac{1}{50}$ sec.

cause a contraction, the summation time on repeated stimuli is much longer (about 50σ) than that for two shocks (10σ).

Action currents have been recorded during summation in both species. The mechanical contraction (isometric) was observed at the same time. It was found that induction shocks which alone cause no contraction, but which did when summated in the way described above, invariably elicited an action current in the muscle. When no action current resulted from either of the two induction shocks, none was obtained when they were summated. With longer intervals between two effective shocks the action currents obtained consist of two separate tops, of which the

second is the higher, which is in accordance with the results obtained on faradic stimulation. As the interval between the shocks becomes shorter the height of the second action current increases, and with the shortest intervals (about 2σ) these tops merge into one large smooth action current (Fig. 4). Thus the maximum facilitation takes place at high frequencies, more than 500 per sec. Fig. 5 shows the relation between the height of the monophasic action current on the second induction shock and the time interval between the two stimuli. In *Cambarus* such an increase of the height of the second action current was not observed (see van Harreveld & Wiersma, 1936, Fig. 5).

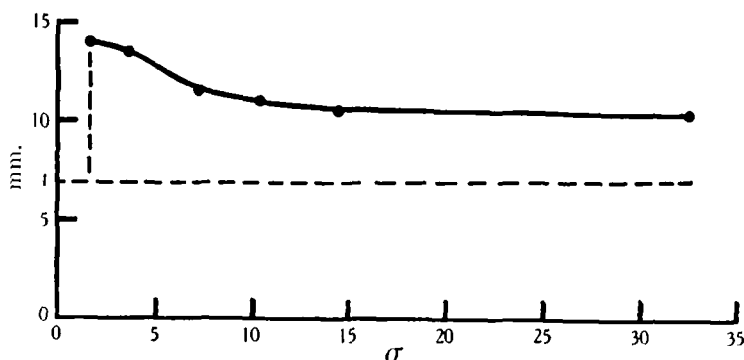


Fig. 5. Curve relating the height of the second spike of the summated action current and the time interval between the two induction shocks in *Blepharipoda*. The line A indicates the height of the action current caused by a single shock.

INDIRECT STIMULATION WITH DIRECT CURRENT

The pseudo-chronaxie of the first mechanical step of the fast contraction of the adductor of *Blepharipoda* and *Randallia* was found to be about 3.5σ (see Table II). This contraction is comparable to the second step of the twitch contraction in the adductor of *Cambarus clarkii* (pseudo-chronaxie 4σ), as both have been proven to be caused by two nerve impulses. In both marine species the maximum contraction of this step causes a tension of 25–30 g., in contrast with that of a number of other marine crustaceans in which this contraction was either very small (*Cancer anthyoni*) or even absent.

The height of the first visible fast contraction varies with the strength of the stimulating current and is about at a maximum in the neighbourhood of the pseudo-

Table II. *Pseudo-chronaxie of the first step of the mechanical contraction*

<i>Randallia</i> σ	<i>Blepharipoda</i> σ
3.2	3.2
3.6	3.8
3.8	3.9
3.6	
2.7	
3.4	

chronaxie strength of the current. Currents of lower voltage give much smaller contractions, and if low enough, the contraction is barely visible. This makes doubtful the measurement of the rheobase; especially as stimuli of voltages, so low that they require a stimulation time of about ten times the chronaxie (e.g. 30σ), do

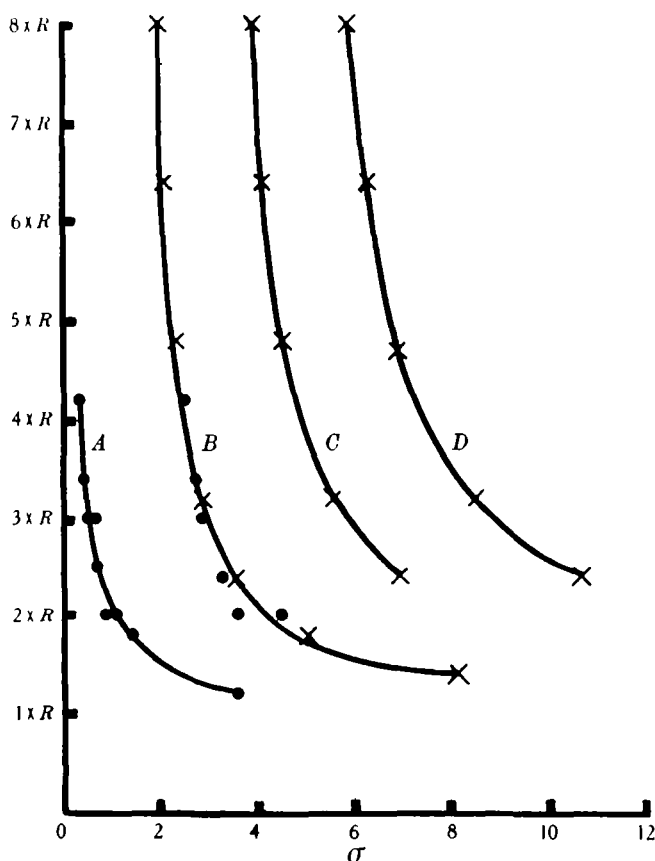


Fig. 6. Strength-duration curves of the adductor of *Randallia* on indirect stimulation; *A* that of the first muscle action current, *B* that of the first visible contraction (crosses) and the action current build up of two tops (dots). *C* and *D* those of the second and third steps of the mechanical contraction respectively. Unit on the ordinate is the rheobase of the first muscle-action current.

not give this contraction at all. Thus the rheobase can be obtained only by extrapolation from the strength-duration curve.

To be sure that the contraction used for the first point of the strength-duration curve belongs to the first visible step, we measured the minimum voltage necessary to give a contraction on a stimulus of a duration of 2.5σ . As the second visible step of the twitch, even stimulating with currents of about ten times the "rheobase" voltage, needs a stimulation time of about 4σ , this contraction can never be elicited by the strength of stimulation used by applying it for only 2.5σ . Other points of the curve could then be easily obtained by gradually changing the strength of the stimulus.

This procedure was not necessary for the rheobase measurements of the second step of *Homarus vulgaris* (Wiersma, 1933) and of *Cambarus clarkii* (van Harreveld & Wiersma, 1936). Though in these latter species small changes in height may occur in the range of the stimulation times used, it was always easy to recognize each step by its height, even on stimulation near the rheobase.

The action currents with direct current stimulation show the features which might be expected from the results with the summation of two induction shocks. There appears an action current which has a much shorter chronaxie than was found for the mechanical contraction; this chronaxie was 0.8σ . In Fig. 6 we give the strength-duration curves of the first and second electrical phenomena and those of the first, the second, and the third steps of the mechanical contraction. The height and shape of the first action current are independent of the strength of the stimulating current. If the duration of the current is increased, a sudden increase of the action current takes place. As can be seen from Fig. 5 this change in the action currents has exactly the same strength-duration curve as the first visible contraction.

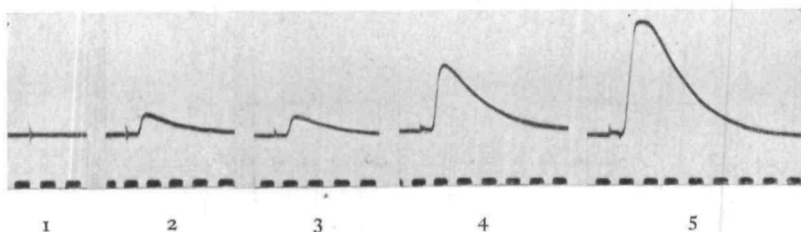


Fig. 7. Action currents on stimulation with direct currents of short duration in *Randallia*. Strength of the stimulus 0.6 V. In 1 the duration of the stimulus is 0.4σ , no action current results. In 2 the duration is 0.5σ , a small action current occurs. In 3 the duration is 3.6σ , the action current is of the same height as in 2. In 4 the duration is 4.5σ ; a higher spike occurs, which accompanies the first step of the mechanical contraction. In 5 the duration is 9σ ; this gives a still higher action current, which accompanies the second step of the mechanical contraction. Time $\frac{1}{10}$ sec.

On stimulating with strong currents this action current is quite smooth (Fig. 7, No. 4); with weaker currents it consists of two clearly distinguishable tops (Fig. 8 C). As in the summation experiments (Fig. 4) the second top of the action current is higher than the first one and this difference reaches its maximum with strong currents.

With each following step of the contraction another top is added to this action current. Eliciting one of the higher steps with a strong short current we obtain a very high smooth spike as the action current (Fig. 7, No. 5); with weaker and longer stimuli the action current of the same step consists of several clearly distinguishable tops (Fig. 8 D).

Since the time intervals between the strength-duration curves of the different steps are almost constant for a stimulation strength of higher intensity (see Fig. 5), it is evident that nerve impulses are set up at regular time intervals by these stimuli.

Stimulation of the whole nerve with direct current of very long duration causes an action current in the adductor muscle in which two parts can be clearly distinguished (Fig. 8). Besides the action current of the fast contraction there appeared

under these circumstances a regular sequence of the much smaller tops of the slow contraction. Sometimes on making the stimulating current very weak these could be obtained without the preceding fast action currents (Fig. 8 A).

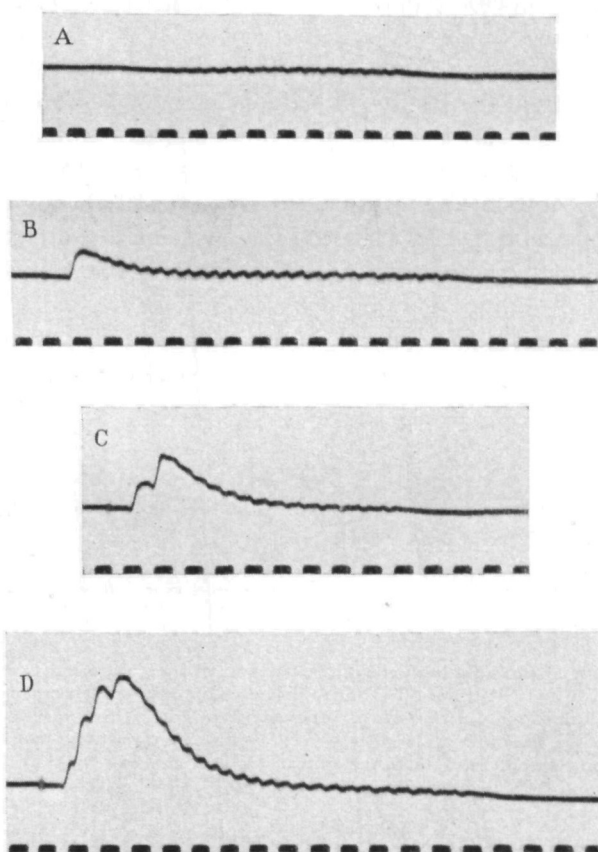


Fig. 8. Same preparation as of Fig. 7, stimulated with direct currents of long duration. In *A* the strength of the stimulating current is 0.2 V.; action currents of the slow contraction only (notice the growth of the action current). In *B* the strength of the current is 0.25 V.; the action current of the slow contraction is preceded by one spike of the action current of the fast contraction. In *C* the strength of the stimulating current is 0.28 V.; two spikes of the action current of the fast contraction which are separate as the stimulating current is weak (compare with No. 4 of Fig. 7). In *D* the strength of the stimulating current is 0.3 V.; the action current of the fast contraction shows 4 tops. Time $\frac{1}{50}$ sec.

CHRONAXIE OF THE NERVE

To show that the first action current of the muscle, which does not yield any mechanical effect, is caused by one nerve impulse, we measured the chronaxie of the whole nerve or of a small fibre bundle containing the motor fibres for the adductor muscle. The nerve action current was taken as an indication of the effectiveness of the stimulus. The chronaxie of the nerve of *Randallia* was thus found to be between 0.5 and 1.0 σ .

THE ADDUCTOR OF THE DACTYLOPODITE OF THE WALKING LEG OF *CANCER ANTHONYI* (RATHBURN)

According to Pantin (1936) who has worked mostly with the adductor of the walking leg of *Carcinus maenas*, the muscles of crustaceans, with the exception of the adductor of the "crusher" claw, are innervated by only one kind of motor axon. We do not claim that every muscle has the double motor innervation; for we have proved that the abductor of the dactylopodite and the extensor of the propodite in the claw of *Cambarus clarkii* are innervated by only one motor axon (van Harreveld & Wiersma, 1937), but we consider this as perhaps a rather rare exception to the rule since we have found the triple innervation in methylene blue stained preparations of a number of muscles of different marine crustaceans. In fact, all the muscles so far investigated (four muscles in the cheliped of *Blepharipoda occidentalis*, including the abductor and the extensor of the propodite, five muscles in the walking leg of

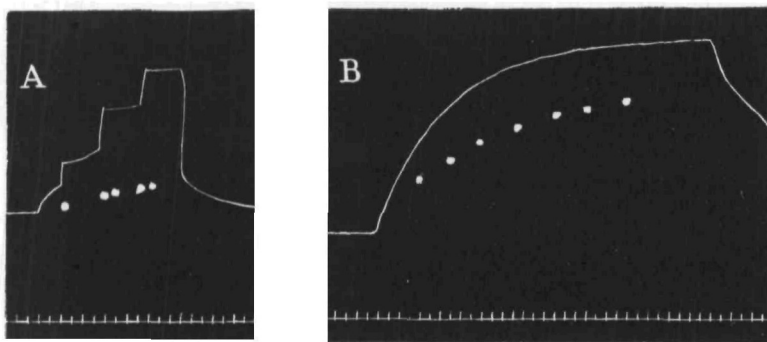


Fig. 9 The experiment of Blaschko *et al*; stimulating simultaneously with a weak faradic stimulation and induction shocks (indicated by the dots), *A* the fibre for the fast contraction, and *B* the fibre for the slow contraction in *Cancer anthonyi*. In *B* there is hardly any effect of the extra induction shocks, but in *A* the contraction often increases suddenly. Time 1 sec.

Cancer anthonyi, including the same muscles, and four muscles in the cheliped of *Pagurus ochotensis*, including the extensor of the propodite) show, without exception, the triple innervation. In the adductor and in the flexor of the propodite in the cheliped of *Blepharipoda*, and in the same muscles in the walking leg of *Cancer*, the double motor innervation has also been demonstrated physiologically.

Of these, the adductor muscle of the walking leg of *Cancer* has been more extensively investigated. The motor fibres were prepared in the usual way. With faradic stimulation (frequency 40–50 per sec.) the thicker of the two fibres gave a smaller and slower contraction than the thinner one. The higher the frequency the less this difference became. At 100 per sec. the two contractions are about the same except that the contraction elicited by means of the thin fibre has the longer latent period (e.g. in a certain preparation the latent periods were 40 and 90 σ).

A contraction can be obtained by the summation of two induction shocks applied in the way described previously over a long range of intervals of summation (1.5 to more than 30 σ). If the two nerve fibres are isolated, and each of them is tested in

this way, the thick fibre gives the same effect as the whole nerve, whereas the thin fibre does not yield a contraction, though faradic stimulation of the same strength showed that the stimulus is effective.

In connexion with this result we have repeated the experiment of Blaschko *et al.* (1931) but on each fibre separately. They stimulated the whole nerve faradically with low frequencies and saw that extra single induction shocks often gave a twitch-like increase of the sustained low contraction, though these shocks given alone did not have any effect. Performing this experiment on the isolated thick

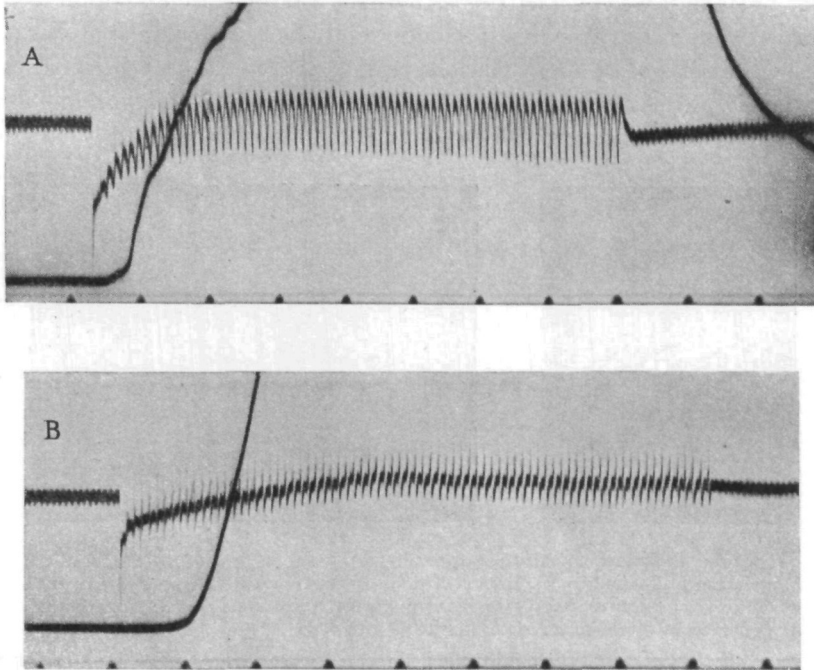


Fig. 10. Mechanogram and electrogram of the adductor muscle of the walking leg in *Cancer anthonyi* stimulating the thick (A) and the thin (B) motor fibre with a frequency of 48 per sec. Note the faster contraction on stimulation of the thin fibre, which has a longer latent period. The action currents on stimulation of the thick fibre start small, and show a marked growth, but are at corresponding moments larger than those of the slow contraction. Time $\frac{1}{2}$ sec.

fibre we obtained a result like that of these authors—that is, the extra stimuli often caused a marked sudden increase in the sustained contraction (Fig. 9). On similar stimulation of the thin fibre these single-induction shocks never gave significant changes.

The difference between the slow and the fast contraction is most distinct in the action current. As in *Blepharipoda* both grow on repeated stimulation; in this case the fast-action current starts out rather small though always visible, whereas the slow-action current is invisible on the first stimuli (Fig. 10). With higher frequencies the action currents of the slow contraction grow to a larger size than the first spike of the fast contraction, which does not take place in *Blepharipoda*.

Stimulating with certain frequency the action currents of the fast contraction are always larger at a definite time of stimulation than those of the slow contraction after the same time, though the mechanical response may be larger during the stimulation of the fibre for the slow contraction.

DISCUSSION

The foregoing experiments have shown without doubt that in the marine crustaceans examined there exists a double motor innervation. The relation between fast and slow contraction in the adductor varies among these species and also differs from that in *Cambarus*. Mechanically the fast contraction becomes slower from *Cambarus* to *Randallia-Blepharipoda* to *Cancer*, so that the difference between slow and fast contractions becomes more difficult to see. It is no wonder therefore that other investigators (Pantin; Katz, 1936) have denied the existence of a double motor innervation. When instead of the two fibres separately both together are put on the electrodes, and the frequency of stimulation is gradually increased, the contraction also increases gradually, and there is no sign of a break caused by the sudden appearance of the fast contraction. Such a break can hardly be expected, however, as is shown by the fact that stimulation of the fibre for the fast contraction alone with low frequencies gives low and slow contractions which grow gradually with increased frequency. Thus the absence of a break is certainly not in contradiction with the existence of two kinds of contraction, as has been claimed by Pantin (1936).

In every case investigated as yet, the action currents have shown a more pronounced difference between the fast and the slow contraction than the mechanical response. Like the mechanical fast contraction the differences in the two kinds of action currents seem to become less in the same sequence of species, as is shown, for example, by the fact that the first top of the fast-action current becomes smaller in relation to the height of the facilitated slow-action current. Furthermore, the fast-action currents, which do not show facilitation in *Cambarus*, show some in *Blepharipoda* and considerable in *Cancer*, so that also in this respect the difference between slow and fast contraction becomes less. The question may be raised whether the double motor innervation in an animal such as *Cancer* has much biological significance, as we have shown that only at high frequencies does stimulation of the thick fibre cause a contraction which is faster than the slow contraction set up by the same frequency. There is, however, always the shorter latent period of the fast contraction which might be of advantage to the animal. It should be further noticed that we may have worked under circumstances in which the latent period of the slow contraction was considerably shortened compared with that of a resting muscle, as repetition of the stimulation shortens the latent period of this system, which has a long after-effect. That the functional difference between the two systems can be larger than the frequency curves show is demonstrated in our variation of the experiments of Blaschko *et al.* (1931). Stimulation of the thick fibre in *Cancer* shows that a single impulse intercalated in a series of impulses is

sufficient to cause a very sudden increase of the contraction. To produce such an effect during the stimulation of the thin fibre it would be necessary to intercalate at least several impulses, and even then the latent period of the increase of the contraction would be longer.

The questions, whether the two kinds of contraction take place in the same muscle fibre, and whether the muscle fibre follows the all-or-none relation or not, will be discussed in a future paper.

SUMMARY

A double motor innervation has been shown for several muscles of marine crustaceans. The adductors of the claws of *Randallia* and *Blepharipoda* and the adductor of the dactylopodite of the walking leg of *Cancer* were studied physiologically.

The two motor axons which innervate these muscles have a different diameter (ratio 1.4:1). Stimulation of the thick fibre causes a response, which, though it is not always faster than the response of the thin fibre, must be considered as a "fast" contraction. In *Randallia* and in *Blepharipoda* the slow contraction is higher than the fast with frequencies of less than ± 50 per sec., in *Cancer* with frequencies less than 100 per sec.

The action currents of the two kinds of contraction are different. Both show facilitation, but under the same conditions of stimulation the fast-action currents are higher. The first stimulus of the thick fibre causes an action current top which is clearly distinguishable, the action currents of the slow contraction show up only after a number of stimuli. Even when the mechanical reaction on stimulation of the thick fibre is smaller than on similar stimulation of the thin fibre, the action currents are higher in the first case.

A single impulse in the thick fibre does not cause a contraction, but sets up a muscle-action current. The chronaxie of this action current in *Blepharipoda* and *Randallia* is 0.8σ and is about the same as that found for the action current of the nerve. Two impulses in the thick fibre may cause a mechanical response, as is shown by summation experiments. The pseudo-chronaxie of this contraction was measured as 3.5σ . The second action current shows facilitation, when it follows the first within 1 sec.; a mechanical reaction results with summation intervals of two stimuli of less than 10σ . The facilitation of the action current increases with decrease of the time interval between the two impulses; with the shortest intervals that give summation the resulting action current is a smooth high spike.

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